Research Article

Effects of Livestock Grazing on Nesting Sage-Grouse in Central Montana

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ABSTRACT Grazing by domestic livestock is ubiquitous in the sagebrush (Artemisia spp.) biome of western North America. Widespread, long-term population declines in greater sage-grouse (Centrocercus urophasianus) have elicited concern about negative effects of livestock grazing on sage-grouse populations. Hypothesized relationships, mostly untested, between livestock and sage-grouse nesting ecology have played a prominent role in shaping public land livestock grazing policy and broader discussions about management of grazing in sagebrush ecosystems. We tested predictions arising from several commonly hypothesized mechanisms by which livestock may affect nesting habitat quality for sage-grouse in a grazed landscape in central Montana, USA. We employed Bayesian variable selection methods to identify factors related to both nest site selection and nest success, focusing on indices of livestock use at local and pasture scales and including other factors known to influence nesting ecology such as anthropogenic features and weather. In spite of some evidence nest survival was positively associated with senesced vegetation height, evidence for effects of livestock presence and indices of local livestock use on nest site selection and survival was equivocal at best. In contrast, we found strong evidence that females selected nest sites based on relatively static features such as sagebrush cover and distance from gravel and paved roads, whereas nest failure was driven primarily by extended periods of heavy precipitation. Management of sage-grouse nesting habitat in this region should focus on conserving areas of adequate shrub cover and preventing further fragmentation by roads. ó 2018 The Wildlife Society.

KEYWORDS Centrocercus urophasianus, greater sage-grouse, habitat selection, livestock, nest survival, northern Great Plains, roads, weather.

Greater sage-grouse (Centrocercus urophasianus), ground-nesting sagebrush (Artemisia spp.)-obligate birds of the western United States and Canada, have declined in abundance since population surveys began in the mid-20th century (Connelly and Braun 1997, Schroeder et al. 2004). Historical and ongoing loss and fragmentation of sagebrush-dominated landscapes from conifer encroachment, invasive annual grasses and fire, sagebrush eradication, cropland conversion, urbanization, and infrastructure are largely responsible for reducing the occupied range by nearly 50% (Knick et al. 2003, Schroeder et al. 2004, Aldridge et al. 2008, Miller et al. 2011, Wisdom et al. 2011). However, even populations in relatively intact landscapes have declined (Nielson et al. 2015, Edmunds et al. 2017), suggesting factors such as disease and fine-scale habitat degradation may still pose widespread threats. Though sparsely populated by humans, sage-grouse habitats nonetheless contain economically important resources including renewable and non-renewable energy sources and livestock forage. Identifying causes of reduced reproduction or survival will help managers implement steps to reverse population declines and obviate the need for protections under the Endangered Species Act that could trigger broad restrictions on land use.

Domestic livestock grazing occurs throughout the range of sage-grouse and has been suggested as a potential contributor to declines (Connelly and Braun 1997, Monroe et al. 2017). Historically, poorly managed livestock grazing contributed to widespread changes in sagebrush vegetation communities with negative implications for sage-grouse habitat quality, including spread of exotic annual grasses, decreased perennial grass cover, and increased dominance of shrubs (Mack 1981, Chambers et al. 2007, Boyd et al. 2014). However, greater understanding of rangeland ecology in conjunction with environmental laws guiding administration of public lands grazing have improved range condition throughout the western United States (Holechek 2011), and evidence suggests complete removal of grazing is unlikely to reverse

legacies of historical overuse (West et al. 1984; Manier and Hobbs 2006; Davies et al. 2009, 2016). Thus, relevant discussions of contemporary effects of livestock grazing on sage-grouse focus on shorter-term impacts of herbivory and presence of grazing animals on sage-grouse behavior and vital rates. For example, positive associations between the height of grass surrounding the nest and nest success have indirectly implicated livestock grazing as a potential cause of increased nest predation (Gregg et al. 1994, Connelly et al. 2000, Doherty et al. 2014). Further, it has been suggested that the presence of livestock near nests may increase nest abandonment (Rasmussen and Griner 1938, Patterson 1952, Coates et al. 2008) and that presence of cattle attracts common ravens (Corvus corax), a major nest predator of sage-grouse, and may thereby increase nest predation (Coates et al. 2016).

However, few studies have directly tested for links between grazing and sage-grouse demographic rates (Dettenmaier et al. 2017). A recent study found a broad-scale association between reported levels of early season grazing and sage-grouse population growth and suggested grazing before or during the nesting and brood rearing seasons may reduce hiding cover critical for successful reproduction (Monroe et al. 2017). Other recent studies, however, suggest the association between herbaceous hiding cover and nest success in sage-grouse may have been overestimated in previous analyses, as many used methods susceptible to producing spurious inference (Gibson et al. 2016, McConnell et al. 2017, Smith et al. 2018b). Others have found that forage utilization levels far beyond what is generally observed in sagebrush ecosystems would be required to substantially reduce hiding cover available to birds nesting beneath shrubs (France et al. 2008). Thus, additional tests for effects of livestock grazing on nest success at meaningful scales are needed to inform management.

We studied sage-grouse nests in a grazed landscape in central Montana, USA, to test for effects of livestock grazing on nest success, a key demographic rate for population growth (Taylor et al. 2012) that is the focus of several hypothesized relationships between livestock grazing and sage-grouse demography (Beck and Mitchell 2000). Our objectives were to quantify evidence for the following hypotheses: livestock use is negatively associated with nest site selection, herbaceous vegetation height and cover is positively associated with nest site selection and nest success, and livestock use within pastures or in close proximity to nests during the nesting season is negatively associated with nest success. We also tested for effects of anthropogenic disturbance, primarily roads and cropland in our study area, and weather to facilitate comparison of effect sizes among grazing variables and other factors related to sage-grouse nesting ecology.

STUDY AREA

Our study area in central Montana (46.4488N, 108.5438W, 3,500 km^2; Fig. 1) is characterized by rolling topography and elevations ranging from 975 m to 1,250 m. Climate in the region was cold semi-arid, with average maximum daily temperature in Roundup, Montana (1981–2010) ranging from 2.88C in December to 30.88C in July and annual precipitation averaging 359 mm (National Centers for Environmental Information 2017). Annual precipitation during the study ranged from 265 mm in 2012 to 485 mm in 2014 (Fig. S1, available online in Supporting Information). Vegetation was characterized by Wyoming big sagebrush (Artemisia tridentata wyomingensis) and silver sagebrush (A. cana) co-dominant with a mix of rhizomatous and caespitose perennial grasses. Dominant grazers included domestic cattle (Bos taurus) and sheep (Ovis aries), pronghorn (Antilocapra americana), desert cottontails (Sylvilagus audubonii), white-tailed jackrabbits (Lepus townsendii), meadow voles (Microtus pennsylvanicus), and grasshoppers (order Orthoptera). Common predators of sage-grouse or their nests included coyotes (Canis latrans), bobcats (Lynx rufus), badgers (Taxidea taxus), red fox (Vulpes vulpes), and common ravens. Other Galliformes included sharp-tailed grouse (Tympanuchus phasianellus) and grey partridge (Perdix perdix). The study area encompassed 30 sage-grouse leks with >1 displaying male recorded in ▢1 year between 2011 and 2016 and spanned portions of 2 state-designated core areas of high sage-grouse abundance. Median high male counts on area leks ranged from 7 in 2014 to 25 in 2016.

Primary land uses in the study area were livestock grazing and dryland farming. Rotational grazing systems were implemented on 10 area ranches during the study (details in Smith et al. 2018a). These grazing systems, administered through the United States Department of Agriculture's Natural Resources Conservation Service (NRCS), were designed to increase hiding cover and food availability for sage-grouse and adhered to a set of common standards. Stocking rates were set to achieve <50% utilization of current year's growth of key forage plants, duration of grazing was limited to <45 days, and season of use was changed each year such that there was at least 20 days between the current year's turn-in and the previous year's turn-out dates if season of use was delayed or between the current year's turn-out and the previous year's turn-in dates if season of use was advanced. Most participating ranches elected to rest ▢20% of identified sage-grouse nesting habitat on an annually rotating basis. Rested pastures were left ungrazed for 2 full nesting seasons. Non-participating ranches used a variety of management strategies but in general were managed less intensively (i.e., with a season-long grazing strategy or slower rotations through larger pastures, usually without annual changes in season of use). Two ranches in the study area grazed cattle and sheep and the rest grazed cattle exclusively; our study is therefore most relevant to cattle grazing. Ten percent of the study area was in cropland. The data presented here were collected from April 2011 to August 2016.

METHODS

Field Methods
We captured female sage-grouse using spotlights and hoop netting from all-terrain vehicles (Wakkinen et al. 1992) from
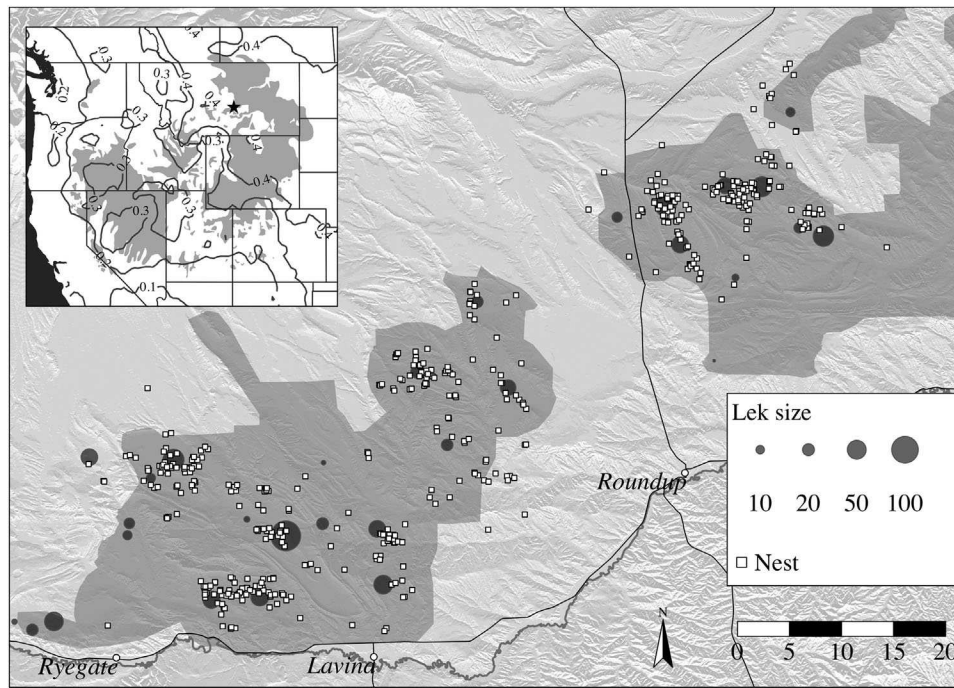
Figure 1. Study area in central Montana, USA. Greater sage-grouse core areas are indicated by gray polygons and leks are indicated by black circles, with size of circles proportional to the highest male count recorded from 2011–2016. Inset map shows location of study area (star) within the current range of sage-grouse (gray shading), and isopleths indicate the average proportion of annual rainfall occurring between 1 April and 31 June.

March to April in 2011–2016 and August to September in 2012–2015 and affixed 25-g necklace-style very high frequency (VHF) transmitters (Advanced Telemetry Systems, Isanti, MN, USA) to captured females. We monitored pre-nesting females at least twice weekly until they began to make localized movements indicative of nesting behavior, at which point we reduced our monitoring interval to daily if possible. We attempted to locate nests from a distance of 10 m without flushing females. We marked nests with inconspicuous natural materials at a distance of approximately 10 m and thereafter monitored nests every 2–3 days from a distance of 100 m. We classified nests as successful (hatched egg with membrane detached) or failed (all eggs destroyed or missing) once the female moved away from the nest. All animal handling was approved under University of Montana's Institutional Animal Care and Use Committee (Protocol 011-14DNWB-031914).

We returned to nests following cessation of incubation activity to measure vegetation, grazing, and anthropogenic disturbance attributes. We made identical measurements at locations randomly generated in a geographic information system (GIS) to quantify resources available to nesting females. In drawing these samples, we imposed several criteria relevant to the behavior of female sage-grouse selecting a nest site (third and fourth order; Johnson 1980). We generated available points within 6.4 km of leks from which we captured females because other studies have shown the large majority of nests are placed within this distance (Holloran and Anderson 2005, Coates et al. 2013). We further constrained available points to areas with 5% visually-estimated sagebrush canopy cover at the plot scale

(30 m) because the importance of sagebrush as a nest substrate and sagebrush cover surrounding nests have been firmly established by numerous studies of nest site selection in sage-grouse (Hagen et al. 2007). At points meeting these criteria, we selected the nearest sagebrush shrub 30 cm in height to designate the nest shrub (Connelly et al. 2000). We sampled 2 available points for each nest.

Model Covariates

We examined covariates falling into 4 categories: local-scale vegetation surrounding the nest, livestock grazing variables, anthropogenic disturbance, and weather (Table 1). We screened candidate variables for collinearity using condition indices (Belsley et al. 1980). If we observed a condition index > 30, we examined the variables implicated by high (> 0.5) variance decomposition proportions and removed them one at a time, retaining the variable with the simplest biological interpretation, until all condition indices were < 30 (Belsley et al. 1980). Because one of our primary goals was to elucidate the relative effect sizes of variables across categories, we scaled and centered all variables to 0 mean and unit variance before fitting models.

Local-scale vegetation.—We established vegetation plots at nests and available points with 2, perpendicular 30-m tapes intersecting at the nest shrub. We estimated canopy cover of sagebrush and other shrubs with the line intercept method along both tapes (Canfield 1941, Wambolt et al. 2006). We estimated cover of understory vegetation, height of live and senesced grasses, and height of shrubs with measurements taken at 8 points located 3 m and 6 m from the plot center in each cardinal direction. We estimated understory cover and

height at this scale because previous research found relationships between herbaceous vegetation structure and nest site selection and success were strongest at a similar scale (7.5 m; Aldridge 2005). At each of these 8 points, we used a 20 × 50-cm quadrat (Daubenmire 1959) to estimate absolute percent cover of understory herbaceous vegetation, litter, and bare ground. We made absolute cover estimates beneath the shrub canopy and included only the uppermost canopy when overlapping canopies occurred. We recorded the maximum vertical height, excluding inflorescences, of undisturbed live and senesced material on the nearest grass plant, and the tallest live portion, excluding inflorescences, of the nearest shrub. A single lead observer trained all technicians to estimate cover each year and periodically checked throughout the season for consistency (i.e., individual estimates within 5% for all cover classes). We estimated visual obstruction with a Robel pole (Robel et al. 1970) placed in the nest bowl and at points 1 m, 3 m, and 5 m from the nest shrub in each cardinal direction, taking readings from 4 m at a height of 1 m above the ground facing toward the nest bowl (modified from Martin et al. 1997). We averaged the 4 readings from each direction at the nest bowl to quantify visual obstruction at the nest, and averaged the 12 readings 1–5 m from the nest to quantify visual obstruction at the plot. We measured the maximum height (h), maximum width (m), and greatest width perpendicular to the axis of the maximum width (p) of the nest shrub to calculate nest shrub volume using the formula for the volume of a half-ellipsoid ($\frac{2}{3}p\frac{m}{2}\frac{p}{2}h$). When the nest was located beneath > 1 shrub with a contiguous canopy, we treated the shrubs as a single shrub for measurement purposes.

Livestock grazing.—To quantify intensity of livestock presence and grazing during the nesting season, we counted cattle dung pats and estimated the proportion of herbaceous plants grazed within a 15-m radius of each nest shrub or available point. Density of dung pats may be indicative of patterns of forage utilization and vegetation structure in areas grazed by livestock (Bailey and Welling 1999, Roche et al. 2012) but also contains information about livestock presence independent of grazing. We recorded the total number of dung pats and categorized them as current year or previous years, which we distinguished by the level of degradation and oxidation. We used dung pats from the current year to index local use by livestock during the current nesting season because livestock turn-out dates in our study area coincided closely with the beginning of the nesting season. We used counts of dung pats from previous years to index intensity of previous years' livestock use, which we used as a candidate

Table 1. Candidate variables for models relating local vegetation, livestock grazing, anthropogenic disturbance, and weather to nest site selection and nest survival of greater sage-grouse in central Montana, USA, 2011–2016.

Category	Variable	Source[a]	Selection[b]	Survival[b]
Local vegetation	Nest shrub volume	1	yes	yes
	Visual obstruction at the nest shrub	1	yes	yes
	Visual obstruction at the plot	1	yes	yes
	Shrub cover	1	yes	yes
	Herbaceous cover	1	yes[c]	yes[d]
	Shrub height	1	yes[c]	yes[d]
	Live grass height	1	yes[c]	yes[d]
	Senesced grass height	1	yes	yes
Grazing	Cow pat density (previous grazing seasons)	1	yes	no
	Cow pat density (current grazing season)	1	yes	yes
	Proportion of plants grazed	1	yes	yes
	Livestock presence in pasture	1	no	yes
Anthropogenic disturbance	Distance to major road	2	yes	yes
	ln(distance to major road)	2	yes	yes
	Distance to 2-track	1,2	yes	yes
	ln(distance to 2-track)	1,2	yes	yes
	Distance to cropland	3	yes	yes
	ln(distance to cropland)	3	yes	yes
	Cumulative disturbance footprint	4	yes	yes
Weather	Precipitation (daily)	5	no	yes
	Precipitation (previous day)	5	no	yes
	Precipitation (2-day sum)	5	no	yes
	Precipitation (3-day sum)	5	no	yes
	Precipitation (4-day sum)	5	no	yes
	Precipitation (5-day sum)	5	no	yes
	Min temperature (daily)	5	no	yes
	Max temperature (daily)	5	no	yes

[a] Sources: 1 ¼ field measurement; 2 ¼ U.S. Census Bureau Tiger/LINE shapefile (https://www.census.gov/geo/maps-data/data/tiger.html); 3 ¼ U.S. Department of Agriculture National Agricultural Statistics Service Cropland Data Layer (USDA-NASS 2016); 4 ¼ U.S. Geological Survey human footprint (Carr et al. 2017); 5 ¼ DAYMET gridded meteorological data (Thornton et al. 2014).
[b] Was variable a candidate in nest site selection or survival analysis?
[c] Herbaceous cover, live grass heights, and shrub heights were corrected to year-specific median nest initiation date for selection analysis.
[d] Herbaceous cover, live grass heights, and shrub heights were corrected to expected hatch date for survival analysis.

variable in nest site selection models to test whether females avoided signs of heavy livestock use when selecting a nest site. Cattle dung pats may persist in arid ecosystems for up to 6 years (Lussenhop et al. 1982); therefore, previous years' dung pat density represented a relative index of use integrated over the past several grazing seasons (Milchunas et al. 1989). Because dung pats reflect presence of livestock but not necessarily grazing, we also recorded the number of plants exhibiting evidence of grazing during the current year from a sample of 100 randomly selected herbaceous plants, 25 from each quadrant of the plot. Finally, we obtained grazing records from most landowners to determine whether livestock had been present in the pasture at any time during nesting, and observers recorded livestock presence or absence in the pasture at each visit to the nest. Where grazing records were lacking or disagreed with field observations, we used field observations.

Anthropogenic disturbance.—At nests and available points, field technicians recorded distance to the nearest visible 2-track (primitive dirt) road. We used a GIS coverage to estimate distance from each nest or available point to the nearest major (gravel or paved) road and to the nearest 2-track road when field estimates were unavailable. We estimated distance to the nearest crop field, excluding alfalfa, using the Cropland Data Layer (U.S. Department of Agriculture National Agricultural Statistics Service [USDA-NASS] 2016) and parcel boundaries from the Montana Cadastral Mapping Project (Montana State Library 2016). We first built a binary cropland raster indicating all 30-m cells classified as cropland in > 1 year between 2008 and 2016. We then determined the area of each parcel classified as cropland and masked out pixels from the binary cropland raster that were located in parcels with < 4 ha of cropland. This eliminated small fragments of cropland that likely arose from misclassification of other land cover classes in the Cropland Data Layer. We then estimated the distance from each nest or available point to the nearest cropland pixel in the cleaned cropland raster. Finally, we used a disturbance footprint raster (Carr et al. 2017) to estimate the cumulative amount of anthropogenic disturbance in the landscape surrounding each nest or available point. We took the mean percent disturbed from all 90-m pixels within 1 km of the nest or available point.

Weather.—We estimated daily weather conditions experienced by nesting females using the DAYMET daily gridded meteorological dataset (Thornton et al. 2014). For each nest-day, we extracted total precipitation, minimum temperature, and maximum temperature from the DAYMET dataset, estimating values at nest locations using bilinear interpolation from the 1-km resolution rasters. We subsequently used these daily precipitation estimates to derive the previous day's precipitation and temporal moving window variables indicating the total precipitation that fell at a given location in the preceding 2, 3, 4, or 5 days, inclusive.

Model Selection and Fitting

We used Bayesian methods to implement a 2-step model selection and fitting procedure, first selecting from among candidate variables within categories (local vegetation, grazing, anthropogenic features, and weather; Table 1), then bringing supported variables across categories together to assess their support and estimate effect sizes. In both steps, regression coefficients b_j for each variable j were the product of binary indicator variables w_j and continuous effect size parameters u_j (Kuo and Mallick 1997, O'Hara and Sillanpää 2009). We used the joint posterior distribution of the vector w to identify the model with the greatest posterior probability—akin to a top model using an information criterion (e.g., Akaike's Information Criterion; Akaike 1973). Specifically, we used the vector w appearing most often across Markov chain Monte Carlo (MCMC) iterations to identify variables in the top model (Converse et al. 2013). We included variables in the top model from each category in the final, combined-category model fitting step. We placed Bernoulli(0.5) prior distributions on indicator variables, representing no prior information about individual variable importance (O'Hara and Sillanpää 2009). Lastly, we quantified support for variables in the combined-category model using Bayes factors (BF), where we calculated BF_j using the prior inclusion probability (0.5) and posterior mean inclusion probability ($w_j^{posterior}$) as $BF_j = \frac{w_j^{posterior}/(1 - w_j^{posterior})}{0.5/(1 - 0.5)}$ (Smith et al. 2011). The BF is therefore a measure of the ratio of posterior model weight to prior model weight. A BF of 1 indicates that the data provided no evidence for an effect of a variable, a BF $\geq$ 3.2 is indicative of a variable with substantial support, and a BF > 10 indicates strong support (Kass and Raftery 1995). We report Bayes factors and 95% credible intervals (CRI) for all model parameters in the combined-category models, conditional on the top model.

We scaled effect size priors according to the number of parameters in the model at each MCMC iteration such that we held total model uncertainty constant across candidate models. Thus, priors for all u_j were distributed Normal(0, (V/M)$^{1/2}$) where M was the number of non-zero indicator variables and V ~ Gamma(3.29,7.8) such that the marginal prior distributions on nest-site selection probability or daily nest survival probability were approximately Uniform[0,1] (Link and Barker 2006, Smith et al. 2011).

We fit models using JAGS (version 4.2.0, mcmc-jags. sourceforge.net, accessed 19 Feb 2016) implemented via the runjags package (Denwood 2016) in program R (version 3.3.0, www.r-project.org, accessed 3 May 2016). For the first step, we identified top models within each category from 100,000 samples from 2 independent chains after discarding the first 20,000 samples from each chain. We based our inference from the combined-category model on a total of 400,000 samples from 2 independent chains after discarding the first 50,000 samples from each chain. We visually assessed convergence and mixing and calculated Gelman-Rubin convergence statistics (Gelman and Rubin 1992, Brooks and Gelman 1997) for all parameters.

Accounting for Phenology

Recently, the importance of timing of vegetation measurement at nests has received considerable attention (Gibson

et al. 2016, McConnell et al. 2017, Smith et al. 2018b). From 2011 to 2015, we sampled vegetation soon after we determined nest fate (i.e., hatch or failure), which induced a significant bias in timing of vegetation sampling between successful and failed nests. In 2016, we changed our field protocol to sample vegetation at expected hatch date regardless of nest fate. Moreover, timing of vegetation measurement at available points was typically later, on average, than at nests. We therefore used an approach from Gibson et al. (2016) to correct for timing-induced differences in vegetation that could produce misleading inference regarding either selection for or fitness consequences of vegetation structure. Specifically, we fit linear models relating all measured vegetation variables to ordinal date of measurement to identify variables that changed throughout the nesting season because of phenology. For variables displaying a significant trend (P < 0.05 in ⊞ yr), we used a fitted linear mixed effects model, with random intercepts and slopes grouped by year to account for annual variation in phenology, to estimate covariate values at expected hatch date (survival analysis) or median ordinal date of nest initiation for first nests (selection analysis) as in Gibson et al. (2016). We used these phenologically standardized covariate values in model fitting.

Nest Site Selection Model

We fit used-available resource selection function (RSF; Manly et al. 2002, Johnson et al. 2006) models using the logit-link to relate measured covariates to used ($y = 1$) or available sites ($y = 0$). We included only first nests in the used sample because birds may alter nest site selection following nest predation (Marzluff 1988, Chalfoun and Martin 2010). We enforced separate intercepts $b_{0,k}$ for each breeding season k to account for varying prevalence of used nests across years because prevalence was a design parameter rather than a random variable. For each site, i:

$$y_i \sim \text{Benoulli}(p_i)$$

and we modeled p_i as a function of P covariates $x_{i,j}$ for $j = 1, 2, \ldots P$:

$$\text{logit}(p_i) = b_{0;k} + \sum_{j=1}^{P} b_j x_{i;j} + d_r$$

$$d_r \sim N(0; s_r)$$

where $b_j = w_j u_j$ and d_r are ranch-level random effects to account for unmeasured factors affecting suitability or accessibility of ranches for nesting. We placed a flat Uniform[0,50] prior on s_r.

Nest Survival Model

Nest encounter histories consisted of observed nest states y for each day t of observation, where $y_{i,t} = 1$ if nest i was observed alive on day t, $y_{i,t} = 0$ if nest i was observed to have failed (female absent and some or all eggs destroyed), and $y_{i,t} = \text{NA}$ on days when nest state was not observed. Beginning on the first day after the nest was detected,

$$y_{i;t} \sim \text{Bernoulli}(y_{i;t} S_{i;t})$$

We modeled daily survival probability $S_{i,t}$ as a function of P nest- and time-varying covariates using a logit link:

$$\text{logit}(S_{i;t}) = b_0 + \sum_{j=1}^{P} b_j x_{i;j;t} + a_k + d_r$$

$$a_k \sim N(0; s_k)$$

$$d_r \sim N(0; s_r)$$

where $b_j = w_j u_j$ and a_k and d_r are year- and ranch-level random effects included to account for unmeasured temporal and spatial variation in factors associated with nest predation risk. We placed flat Uniform[0,50] priors on s_k and s_r. We previously determined that survival did not vary with nest age or date in this dataset (Smith et al. 2018a); therefore, we did not consider these variables. We derived an estimate of annual nest success by exponentiating estimated daily survival rate from the full model by 37, the typical length of exposure of sage-grouse nests during laying and incubation (Schroeder et al. 1999).

Assessing Model Fit

We performed posterior predictive checks (Gelman et al. 1996, 2014) of our final nest site selection and nest survival models to determine whether the models could faithfully reproduce our observed data. Also called Bayesian P-values, posterior predictive checks are essentially goodness-of-fit tests for Bayesian models that compare an attribute of the observed data to that of data generated by the model. We used the model deviance, D, as a test statistic to assess fit of the nest site selection model (Broms et al. 2016). We calculated the proportion of MCMC samples (s) for which the observed deviance,

$$D^s = -2 \sum_{i=1}^{N} \log(y_i | w; u)$$

was greater than the deviance calculated from new data predicted by the model ($\tilde{y}$):

$$\tilde{D}^s = -2 \sum_{i=1}^{N} \log(\tilde{y}_i | w; u)$$

We used the number of hatched nests to assess fit of the nest survival model. Drawing from the joint posterior distribution, we calculated daily survival probabilities $S_{i,t}$ for each observed nest i on day t from the first date of observation to 27 days after the estimated incubation initiation date, reflecting the typical incubation period. We predicted the outcome, hatch$_i$, of each nest by taking successive Bernoulli draws of nest state $y_{i,t}$ from $S_{i,t}$ until $y_{i,t} = 0$ (failed nest) or until $t = $ estimated hatch date (hatched nest). We then calculated the proportion of MCMC samples for which the observed number of hatched nests was greater than the predicted number. Values near 0.5 indicate the model

RESULTS

We located and determined the fate of 501 nests from 256 captured females from 2011–2016. We removed 4 nests from the survival analysis because of early, likely observer-induced abandonment (Gibson et al. 2015) and removed 2 nests because we found them after predation had occurred. Of the remaining 495 nests, 2 nests (0.4%) were abandoned following predation of the female while off the nest, 10 nests (2.0%) were abandoned for unknown reasons, 229 (46.3%) hatched at least 1 egg and were classified as successful, and predators destroyed 254 nests (51.3%). Median clutch size was 8 eggs for first nest attempts and 7 for second and third nest attempts. When fitting local-scale vegetation models, we excluded 2011 data because of extremely delayed vegetation measurement.

Nest Site Selection

After excluding renests, we used 353 nests and 710 available points for the nest site selection analysis (see Table S3, available online in Supporting Information for means and SDs of variables). Live grass height, herbaceous cover, and shrub height displayed significant temporal trends in year, so we made corrections to these variables before model fitting. All condition indices were < 5, indicating multi-collinearity was not problematic. Nest shrub volume, visual obstruction at the nest, shrub cover, and live grass height appeared in the top local vegetation model (Table S1, available online in Supporting Information. The top grazing model contained only previous years' cow pat density. The top anthropogenic disturbance model contained ln(distance to major road), and ln(distance to 2-track). The top combined-category model included all variables from top categorical models, but Bayes factors indicated mixed support (Table 2). Females selected larger nest shrubs with less visual obstruction, surrounded by greater shrub cover, farther from major roads but closer to 2-track roads relative to available points (BF > 3.2; Table 2 and Fig. 2). Avoidance of high densities of previous years' cow pats received weak support (BF ¼ 2.5; Fig. 2), and evidence for selection for greater live grass height was equivocal (BF ¼ 1.4). The posterior predictive check of the top nest site selection model indicated good model fit (P ¼ 0.52).

Nest Survival

All condition indices were < 5, so we did not remove any candidate variables before model fitting. The top local vegetation model contained effects of nest shrub volume and senesced grass height. The top anthropogenic disturbance model contained only ln(distance to major road). The top grazing model contained only the proportion of plants grazed. The top weather model included total rainfall over a 5-day period. Delayed measurement of vegetation in 2011 was not a major concern because the only herbaceous vegetation covariate in the local vegetation model was senesced grass height, which should be largely unaffected by phenology. Thus, we used all nests (n ¼ 495) to fit the combined-category model. We included visual obstruction at the nest shrub because it appeared in 2 local vegetation models with model weights nearly equal to the top model (Table S2, available online in Supporting Information) and had a mean posterior inclusion probability > 0.5. The top combined-category model included nest shrub volume, senesced grass height, proportion of plants grazed, ln(distance to major road), and total rainfall over a 5-day period. Daily nest survival was positively associated with greater distance from major roads and negatively associated with precipitation over a 5-day period, whereas evidence for the effect of taller senesced grass, nest shrub volume, and proportion of plants grazed was weak (BF < 3.2; Table 3). Variation in daily survival rates among years (s_k ¼ 0.34, 95% CRI ¼ 0.11–1.06) was approximately 5 times greater than variation among ranches (s_r ¼ 0.07, 95% CRI ¼ 0.00–0.24). Holding all covariates at their mean value, mean daily

Table 2. Coefficient estimates and Bayes factors from a logistic regression model describing effects of local vegetation, livestock grazing, and anthropogenic disturbance on nest site selection of greater sage-grouse in central Montana, USA, 2011–2016.

Category	Variable	BF[a]	Posterior distribution[b]		
			Lower 95% CRI	Median	Upper 95% CRI
	Intercept[2012]		−1.45	−1.01	−0.57
	Intercept[2013]		−0.84	−0.36	0.12
	Intercept[2014]		−1.32	−0.85	−0.40
	Intercept[2015]		−1.58	−1.12	−0.68
	Intercept[2016]		−1.00	−0.54	−0.08
	s_r (ranch-level variation)		0.44	0.89	1.51
Local vegetation	Nest shrub volume	18,180.8*	0.25	0.41	0.58
	Visual obstruction at the nest shrub	4.6*	−0.36	−0.20	−0.04
	Shrub cover	> 200,000*	0.30	0.44	0.60
	Live grass height	1.4*	−0.01	0.16	0.32
Grazing	Cow pat density (previous years)	2.5*	−0.33	−0.17	−0.02
Anthropogenic disturbance	ln(distance to major road)	778.7*	0.16	0.33	0.50
	ln(distance to 2-track)	56.3*	−0.38	−0.24	−0.10

[a] BF ¼ Bayes factor; BF values with an asterisk indicate variables appearing in the top model.
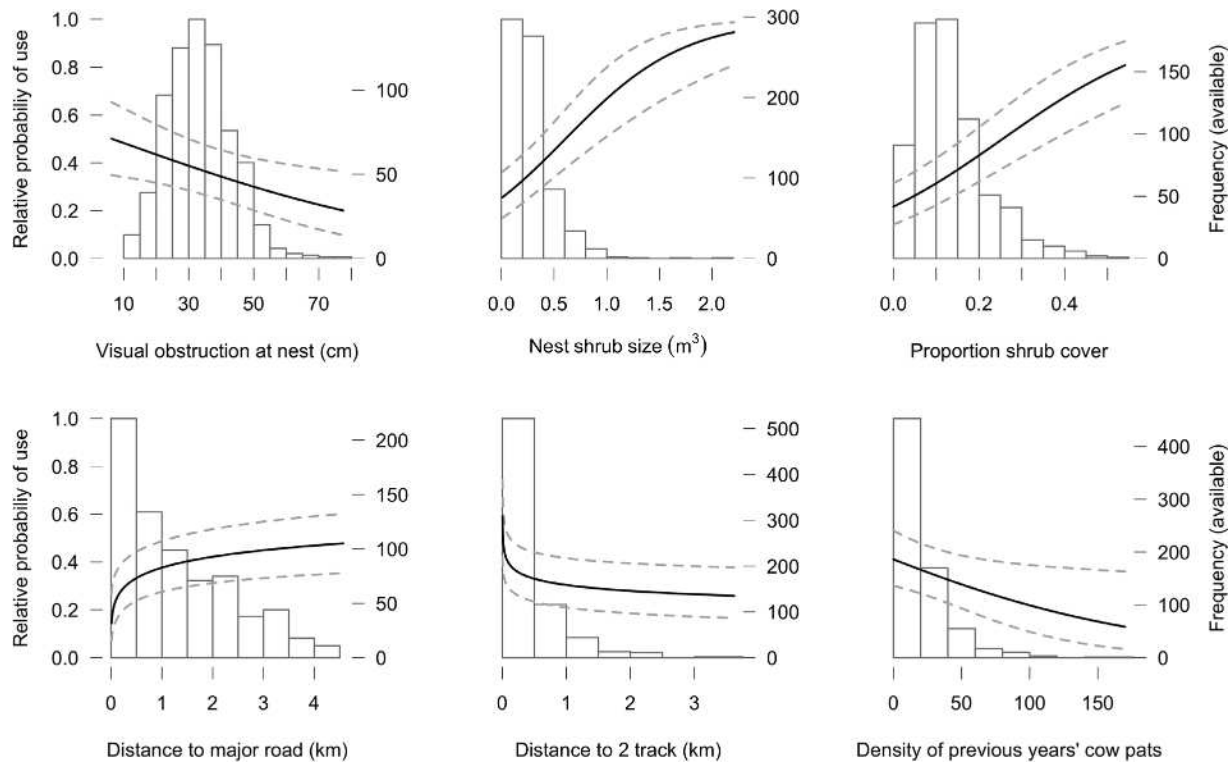[b] Median, lower, and upper credible intervals (CRI) are conditional on the top model.

Figure 2. Predicted relative probability of use and 95% credible intervals among factors influencing nest site selection in greater sage-grouse in central Montana, USA, 2011–2016. Histograms represent covariate values measured at available sites (n ¼ 710).

survival rate of nests was 0.971 (95% CRI ¼ 0.953–0.979). Nest success, assuming 37 days of exposure (Schroeder et al. 1999), was 33.3% (95% CRI ¼ 16.7–46.1%). When we removed the anomalous 2011 data (Fig. S1) from the mean of the precipitation covariate, estimated daily survival rate and nest success were 0.972 (95% CRI ¼ 0.955–0.980) and 34.6% (95% CRI ¼ 18.3–47.0%), respectively. The top combined nest survival model had a Bayesian P-value of 0.46, indicating good model fit.

DISCUSSION

We found little evidence for the hypothesized indirect and direct effects of livestock grazing that were the primary focus of our study. Considered alongside our finding that spatial variation in nest survival among ranches was minor compared to annual variation (Table 3 and see Smith et al. 2018a), variation in grazing management in our study area appears to have only minor effects on sage-grouse nesting ecology. Rather, structural characteristics of the shrub community and anthropogenic features were the primary drivers of nest site selection, whereas periods of prolonged heavy rainfall and proximity to gravel and paved roads had the largest effect on daily nest survival.

We found little evidence that variation in livestock grazing or its effects on herbaceous vegetation was associated with nest site selection. There was weak support for avoidance of

Table 3. Coefficient estimates and Bayes factors from a logistic regression model describing effects of local vegetation, livestock grazing, anthropogenic disturbance, and weather on daily survival rates of greater sage-grouse nests in central Montana, USA, 2011–2016.

Category	Variable	BF[a]	Posterior distribution[b]		
			Lower 95% CRI	Median	Upper 95% CRI
	Intercept		3.00	3.50	3.86
	s_k (year-level variation)		0.11	0.34	1.06
	s_r (ranch-level variation)		0.00	0.07	0.24
Local vegetation	Nest shrub volume	1.6*	−0.01	0.12	0.27
	Senesced grass height	2.8*	−0.00	0.14	0.29
	Visual obstruction at the nest shrub	0.3			
Grazing	Proportion of plants grazed	1.6*	−0.20	−0.10	0.01
Weather	Precipitation (5-day sum)	220.0*	−0.30	−0.20	−0.09
Anthropogenic disturbance	ln(distance to major road)	7.9*	0.03	0.16	0.28

[a] BF ¼ Bayes factor; BF values with an asterisk indicate variables appearing in the top model.
[b] Median, lower, and upper credible intervals (CRI) are conditional on the top model.
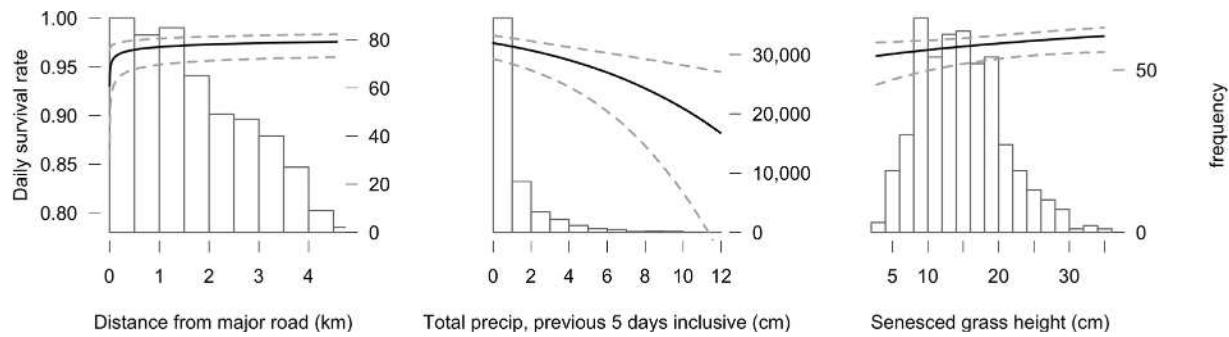
Figure 3. Predicted daily nest survival and 95% credible intervals among factors influencing daily survival rate of greater sage-grouse nests in central Montana, USA, 2011–2016. Histograms represent frequency of covariate values in the dataset.

sites with a high density of previous years' cow pats, but the effect size was small. Though such an association might arise through avoidance of areas of reduced height of senesced vegetation from previous grazing, we considered height of senesced grass as a candidate variable in the nest site selection model and it was unsupported. Regardless of the mechanism underlying this association, preferred sites do not appear to be limiting; we counted zero previous years' cow pats at 60% of available sites (Fig. 2). Furthermore, cattle likely avoided areas characteristic of nesting habitat; cow pat counts and shrub cover were negatively correlated at available points (r ¼ 0.16, P < 0.001). Although selection of sites with greater live grass height appeared in the top combined selection model, a BF of 1.4 was well under the threshold of 3 that Kass and Raftery (1995:777) consider evidential strength "not worth more than a bare mention."

Similarly, none of the proposed grazing variables were strongly associated with nest success. Proportion of plants with evidence of grazing appeared in the top combined survival model, but support for the effect was equivocal (BF ¼ 1.6; Table 3). Though initial model fitting without correcting for phenologically induced differences in grass height (Gibson et al. 2016, McConnell et al. 2017) pointed to a strong, positive association between the height of grasses around the nest and nest survival, this association broke down once we made appropriate corrections (Smith et al. 2018b). We did, however, find some support for a positive association between senesced vegetation height and daily nest survival (Fig. 3). Although evidence for this association was weak (BF ¼ 2.8), this suggests senesced herbaceous vegetation may play some role in concealing nests from predators. A closer examination of the estimated effect size for this parameter may explain why we failed to detect effects of local grazing indices in spite of this. The standard deviation in senesced grass height among nests was 5.8 cm; thus, the estimated coefficient for senesced grass height indicates a 1-cm increase in height was associated with a 2.4% increase in the odds of daily nest survival. Given that the difference in senesced grass height between nests in grazed pastures and nests in pastures without evidence of current year's grazing was < 1 cm (Fig. 4), we would not expect grazing to measurably affect nest outcomes through its effects on vegetation height. The apparent lack of

correlation between annual mean nest survival and annual mean senesced grass height at nests (Fig. 5) is further evidence of the biological insignificance of this effect. Overall, hypothesized links between grazing, hiding cover, and nest success were largely unsupported. Livestock grazing, as conducted across our study area, appears to be compatible with maintaining nest success rates typical of a stable population (Taylor et al. 2012). This conclusion is corroborated by the observation that median high male counts on area leks more than tripled during a stretch of years, 2014–2016, characterized by favorable weather.

Though precipitation has been positively linked to population growth in sage-grouse in the Great Basin (Blomberg et al. 2012), we found extended periods of heavy precipitation strongly reduced nest success (Fig. 3). Our study area experienced large precipitation anomalies during the first 2 years, with 2011 (wet) and 2012 (dry) rivaling or breaking precipitation records dating to the 1940s (Fig. S1;
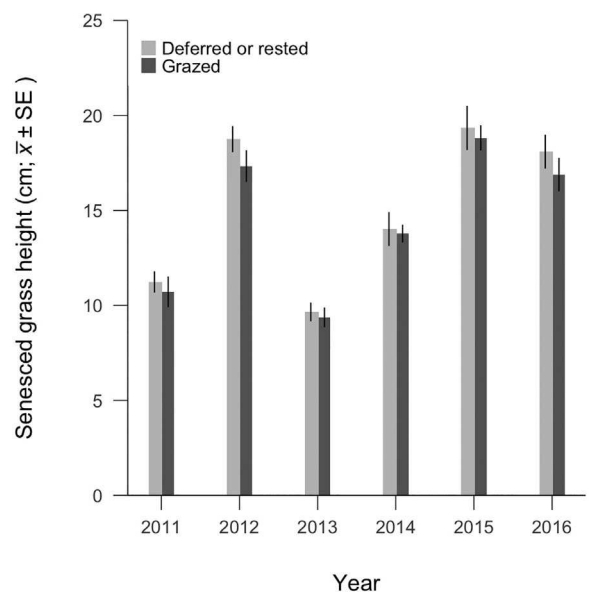

Figure 4. Height of senesced grasses measured within 6 m of greater sage-grouse nests in grazed (n ¼ 273) and deferred or rested pastures (n ¼ 221) in central Montana, USA, 2011–2016. Inter-annual variation, driven primarily by precipitation, was substantially greater than the effect of grazing.
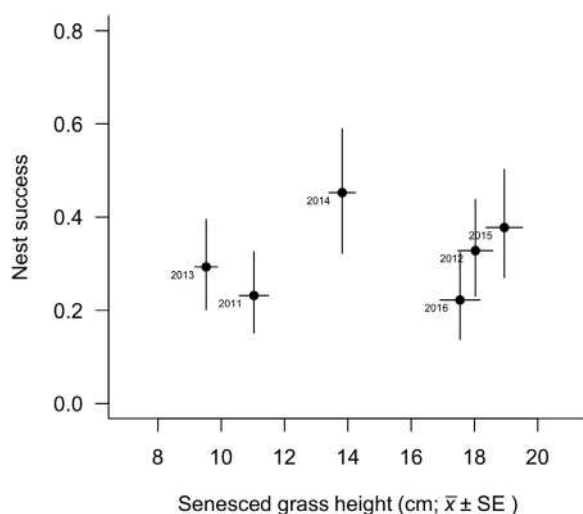
Figure 5. Estimates and 95% credible intervals of annual mean nest success of greater sage-grouse nests in central Montana, USA, 2011–2016. Estimates are from a model with only an intercept and random effect for year and assume an average exposure period of 37 days (10 days of laying and 27 days of incubation). We measured height of senesced grass within 6 m of the nest bowl. Although we found weak support for a positive effect of senesced grass height on daily nest survival, the substantial inter-annual variation in senesced grass height at nests did not correspond closely with annual patterns in nest success.

National Centers for Environmental Information 2017). These extremes likely contributed to the prominence of the precipitation effect in our model. In a post hoc analysis, in which we omitted 2011 nests from the combined-category nest survival model to determine how much this extremely wet year influenced our estimate, we found the effect of precipitation diminished but still supported (BF ¼ 5.6, estimate ¼ 0.16, 95% CRI ¼ 0.29 to 0.03). Thus, although weather may exert weaker effects on nest success in years of historically typical nesting season rainfall, increased frequency of extreme precipitation events across much of the United States over the past several decades may be cause for concern (Karl and Knight 1998). Sage-grouse populations east of the Rocky Mountains, where major rainfall events are more likely to coincide with incubation and brood rearing when grouse are most sensitive to exposure (Fig. 1, inset), may respond differently to annual precipitation than those in the Great Basin, which receives most of the annual rainfall in winter.

Similar to other prairie grouse, negative effects of anthropogenic features on sage-grouse appear to be common (Naugle et al. 2011, Hovick et al. 2014). Avoidance of anthropogenic structures, including roads, by nesting females has been demonstrated (Lyon and Anderson 2003, Dinkins et al. 2014) and our study adds to a growing list reporting negative fitness consequences of nesting near anthropogenic features (Holloran et al. 2005, Aldridge and Boyce 2007, Webb et al. 2012, LeBeau et al. 2014). Major roads appeared to be the feature most responsible for negative effects on nesting grouse in our study area; the cumulative disturbance footprint was a poorer predictor of both nest site selection and nest survival. Reasons for reduced nest survival near

major roads may include reduced ability to detect approaching predators over ambient road noise (Blickley et al. 2012), or increased nest predator abundance or efficiency facilitated by the power lines, culverts, and roadkill that often accompany major roads. The latter mechanisms seem most plausible in our study area because most roads in this class served primarily as travel routes for area ranchers and therefore experienced low traffic volume. Greater support for log-transformed distance to major roads implies negative effects on nest site selection and nest survival diminish after 1–2 km (Figs. 2 and 3). Still, areas far from major roads are uncommon in our study area and in sagebrush landscapes in general (Naugle et al. 2011), and even a 1-km effect distance represents a substantial footprint for these long, linear features.

We found strong support for apparent selection of sites closer to 2-track roads (Table 2), which was contrary to our expectations. This may reflect a true behavior, but we can think of 2 conflating factors that could have produced this result. First, this pattern may simply reflect that terrain characteristics selected by nesting females are similar to those conducive to vehicle travel (i.e., flat or gentle terrain). Second, if technicians had greater familiarity of local road networks surrounding nests, which were typically visited several times for monitoring purposes, than random sites, which were visited only once, then they may have been more adept at locating the nearest 2-track road to nests. Because not all 2-track roads appear in the GIS coverage, this could easily induce a bias whereby field-recorded distances tended to be shorter for nests than random points. In a post hoc test in which we fit the combined selection model using only distances calculated from the GIS roads layer and ignoring field-recorded distances, the apparent selection for proximity to 2-track roads diminished and became statistically nonsignificant (BF ¼ 0.25, estimate ¼ 0.03, 95% CRI ¼ 0.18–0.11). Considered alongside our finding that proximity to 2-track roads was not related to nest survival, our results suggest 2-track roads were benign features for nesting sage-grouse.

Given the established negative association between cropland and lek occurrence and persistence at broad scales (Aldridge et al. 2008, Smith et al. 2016), we were surprised to find no evidence for avoidance of cropland or negative effects of proximity to cropland on nest survival. Lek sites reflect availability of nesting habitat in the surrounding landscape (Gibson 1996) and lek persistence is compromised in landscapes with even small incursions of cropland. For example, 98% of active leks in the western portion of the range were found in landscapes with < 25% cropland in a 5-km radius (Knick et al. 2013) and 96% of active leks in the northern Great Plains had < 15% cropland within 3.2 km (Smith et al. 2016). Spillover effects (Schneider 2001) from cropland into surrounding rangeland seem plausible because common nest predators such as ravens appear to benefit from cropland (Engel and Young 1992, Coates et al. 2016). We therefore expected to find edge effects of cropland on quality of nesting habitat. Instead, although we did not observe any nests in cropland, habitat near cropland edges was used in

proportion to its availability and afforded nest success rates similar to interior habitat. The mechanisms responsible for the broad-scale effect of cropland on sage-grouse distribution are still poorly understood, but our findings do not support the hypothesis that edge effects reduce nesting habitat quality in areas fragmented by cropland. Nonetheless, cropland conversion amounts to loss of nesting habitat, which no doubt contributes to the broad-scale sensitivity of populations to cropland.

MANAGEMENT IMPLICATIONS

We found little indication of short-term negative effects of livestock grazing, as conducted in our study area, on nesting habitat quality. Management interventions such as rest, destocking, or delaying turnout until after the nesting season therefore appear unlikely to increase nest success in this region. We urge caution in extrapolating our findings outside the northern Great Plains, however, as vegetation in other regions occupied by sage-grouse, such as the Great Basin, may respond differently to grazing. Our findings regarding the importance of shrub cover to nesting sage-grouse align with other research from across the range (Hagen et al. 2007) and suggest that shrub control (e.g., to increase forage production or accessibility) is likely to reduce preferred nesting habitat. Among common economic activities in sagebrush ecosystems, ranching is associated with the lowest density of anthropogenic features such as roads (Naugle et al. 2011). In this region, where land is predominantly under private ownership and cropland conversion poses an ongoing threat to populations (Smith et al. 2016), land uses that maintain intact, minimally-roaded native shrublands should be encouraged to ensure the long-term conservation of productive nesting habitat for sage-grouse.

ACKNOWLEDGMENTS

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